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A venomous arthropod in the Early Cambrian Sea

FU DongJing, ZHANG XingLiang* & SHU DeGan

State Key Laboratory of Continental Dynamics, Early Life Institute and Department of Geology, Northwest University, Xi'an 710069, China

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A number of recently evolved animals possess poison glands for feeding and/or defense. However, examples of such animals are rare in the fossil record. We report a fossil arthropod *Isoxys curvirostratus* from the Early Cambrian Chengjiang biota of China. This species is regarded as the oldest known venomous arthropod based on the presence of venomous glands in its head region. The adult animal is 2–5 cm long and the body is covered entirely with a carapace. The presence of large stalk eyes and a pair of stout grasping appendages with a terminal spine suggest it was raptorial. Interestingly, the two pear-shaped, three-dimensionally preserved objects that are present in the head region and at the base of the grasping appendages closely resemble the venom glands of some living arthropods in size, shape, and position. These features indicate that the presence of venomous predators could date back 520 million years. Furthermore, our observations suggest that the feeding strategies and organs adapted for this purpose had already reached a high level of diversity and anatomical sophistication in the Early Cambrian ecosystems.

arthropod, *Isoxys*, venom gland, feeding strategy, Cambrian

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Animals have evolved a range of adaptations for feeding and defense, including the use of poisons and venoms. The use of these toxins is common in many animal phyla, including representatives from very simple organisms up to the advanced vertebrates (e.g. jellyfish, cone snails, spiders, scorpions, centipedes, bees, toads, snakes, stingrays, and duckbills). Despite their current ubiquity, records of venom glands are rare in the fossil record. In particular, little is known about the existence of early predators that used venom. We document a pair of fossilized venom glands (a specific organ that produces and stores toxic substances) in an arthropod *Isoxys curvirostratus* Vannier and Chen, 2000 from the Chengjiang biota [1,2], China. This fossil provides evidence that venomous strategies for feeding had evolved by the early Cambrian (about 520 million years ago). This period coincided with the major morphological and ecological diversification of the Metazoa.

The soft body of the two arthropod specimens illustrated here is entirely encased in a bivalved carapace with strong antero- and postero-cardinal spines. The two specimens are 2.6 cm and >4.0 cm in length, respectively. They are characterized by large stalked eyes, a pair of uniramous grasping appendages with a terminal spine, and a series of biramous limbs (Figures 1a, e and 2). Interestingly, two pear-shaped, three- dimensionally preserved objects, each 0.6 mm in diameter, are present in the head region, immediately posterior to the base of the grasping appendages (Figure 1a,b). These structures closely resemble the venom glands of some spiders in size, shape and position. For example, the black widow spider (*Latrodectus mactans*) has two spherical venom glands located in the head and opening at the base of the chelicerae. Despite the small size of the glands (~1 mm in diameter) relative to the body (body length is typically 1.5 cm, excluding the limbs), they are able to secrete sufficient quantities of venom to kill a number of invertebrates [3]. In addition, the pair of small spheroids in the fossil specimens is easily distinguished from other organs. We argue that they differ in size and location from the digestive/midgut

*Corresponding author (email: xzhang69@nwu.edu.cn)

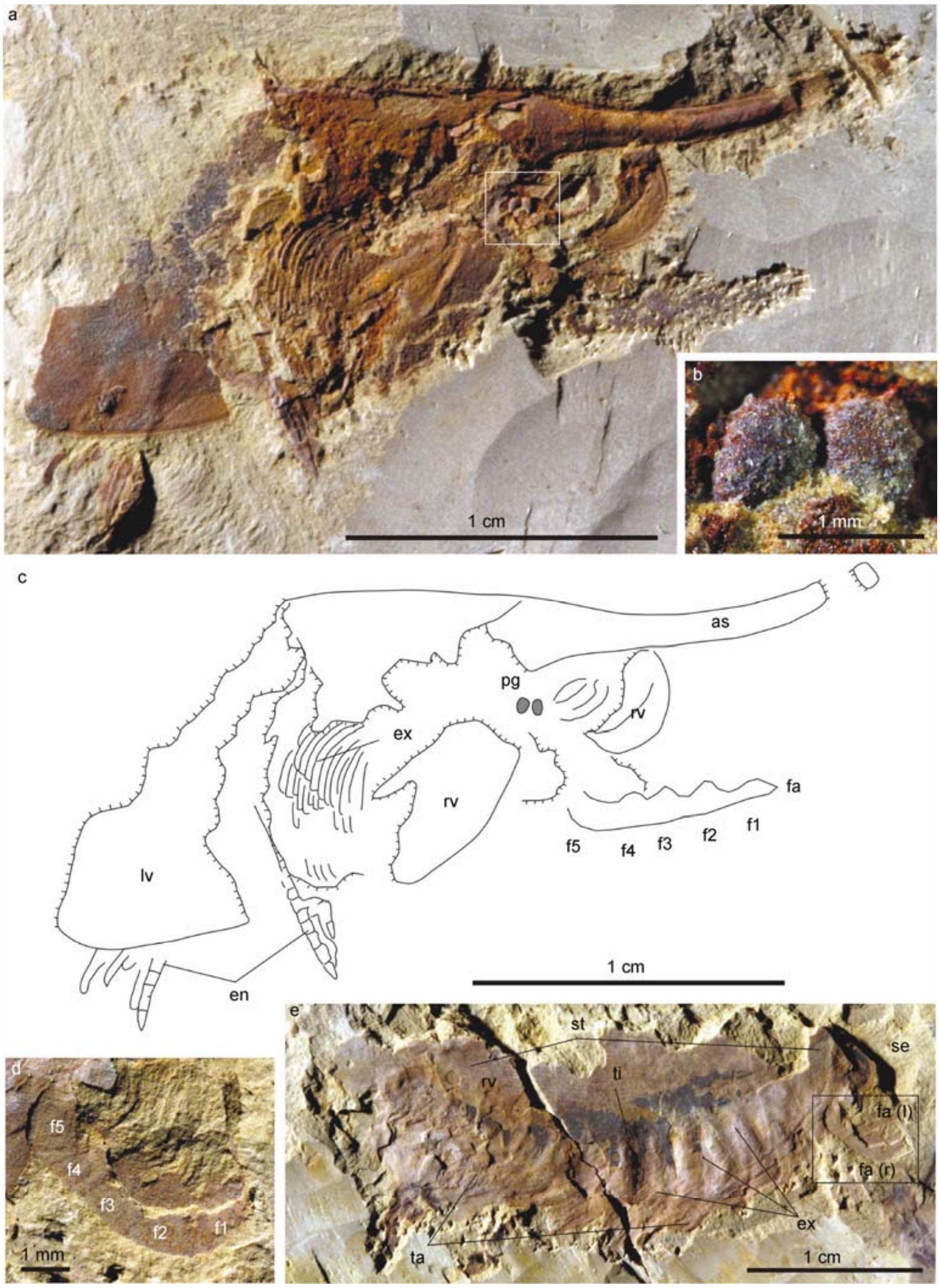

Figure 1 *Isoxys curvirostratus* from the Chengjiang biota, Lower Cambrian, Yunnan, China. (a) Specimen showing the frontal grasping appendage (fa), exopod (ex), endopod (en) and poison gland (pg), JS0008. as, antero-cardinal spine; f1–f5, podomeres of the grasping appendage from the distal to proximal; lv, left valve; rv, right valve. b, Detailed view of two poison glands. c, Camera-lucida drawing of JS0008. d, Detailed view of grasping appendages, showing the intersegmental membranes, five podomeres, and inner outgrowth. e, Specimen showing the striated ornament (st) on the carapace, stalked eye (se), grasping appendages, trunk appendage (ta) and trace of the trunk (ti), JS0014.

gland. The proposed venom glands are positioned towards the anterior (within the cephalon) and are much smaller than the digestive gland, which is equal in size to the exopod [4]. Similarly, the glands are smaller than the stomach, and have a different shape from the brain. It is also unlikely that they represent the median/simple eye based on differences in the potential for preservation (3D preservation is more common for some glands (e.g. midgut gland) than for eyes in the Chengjiang fauna).

The raptorial mode of life has been recognized in *Isoxys* by many authors based on the presence of a pair of capturing appendages that are analogous to the chelicera of Chelicerata in function [5–8]. This, coupled with the presence of venom glands, leads us to conclude that *I. curvirostratus*

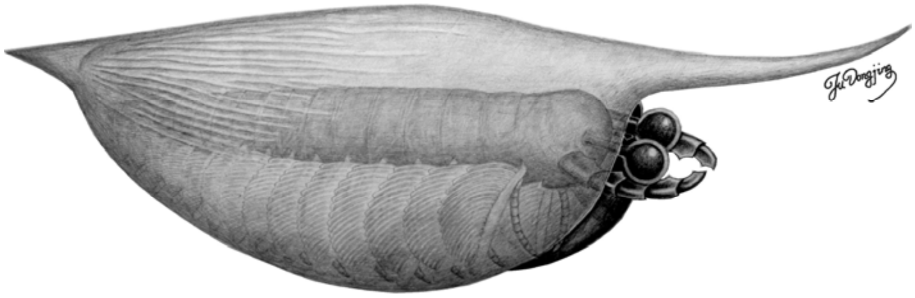

Figure 2 Reconstruction of *Isoxys curvirostratus*.

is a venomous predator. It is very likely that the animal punctured prey with the terminal spine (functioning in a similar way to the fang in spiders and the terminal claw of the maxillae in remipedes [9]) of the grasping appendages following capture and, simultaneously, injected venom into the body of the prey, as suggested by recent analogues. The venom may be delivered by a duct within the grasping appendages. When prey was poisoned to death, the predator may have pumped digestive enzymes from the midgut into the prey then sucked the hydrolyzed fluid, leaving behind a nearly intact husk, i.e. non-durophagous predator. The lack of any bodily material inside the gut in our materials as well as the 3D-preserved digestive glands in similar animals from the Burgess Shale [4] and Emu Bay Shale [10] support this hypothesis.

Predator-prey interactions play a fundamental role in animal evolution and examples date back to the Neoproterozoic-Cambrian transition interval [11]. However, the use of venom by predators has not been documented from the Cambrian fossil record. Our observations suggest that venomous predation has a much earlier origin. Taken together with previously reported evidence [12,13], it is very likely that almost all the feeding strategies known in present-day ecosystems probably existed in the Early Cambrian and organs adapted for this purpose had already reached a high level of diversity and anatomical sophistication.

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